The following papers were read :—

## 1. Contributions to the Osteology of Birds. Part I. *Steganopodes*. By W. P. Pycraft.

[Received February 12, 1898.]

(Plates VII. & VIII.)

It has recently fallen to my good fortune to be set the task of determining and arranging the large collection of birds' skeletons at the British Museum. I propose to embody the results of my work in a series of papers of which this is the first. Before going further, I would like to remind those interested that I shall be most grateful to receive, on behalf of the Collection, embryos, nestlings, and adults of all Orders, for there are many gaps left by imperfect specimens, and otherwise, which much need to be filled up.

The Pelicans, Tropic-birds, Frigate-birds, Cormorants, Darters, and Gannets all agree in one point—all four toes are united in a common web. This fact has been deemed by some of sufficient importance to justify their separation from the rest of the Carinatæ, to form a special group by themselves—the *Steganopodes*. Others, on account of anatomical differences which obtain amongst certain of the groups thus brigaded together, are inclined to doubt whether this separation is a valid one, whether the value of this single external character is sufficiently great to be regarded as a primary dividing factor. The stumbling-blocks which threaten the general harmony are *Phaëthon* and *Fregata*.

I hope, in the present paper, to show that, after all, the "totipalmate" foot may be adopted as the shorthand sign of the group: to show that (1) all are closely related; that (2) they cannot be broken up to form one or more suborders or subdivisions of equal value, but that (3) they must be regarded as a whole, as a suborder or subdivision of some larger group; and that (4) they cannot consistently be merged as a whole with that larger group.

The most important witness to the integrity of the Suborder is the skull. Three types can be easily distinguished:—

1. Basitemporal plate shield-shaped, with a free edge anteriorly forming a floor to the Eustachian tubes, or rather grooves.
2. Basitemporal plate triangular, its lateral borders fused with the basisphenoid, free anteriorly and contributing to form the mouth of the Eustachian aperture.
3. Basitemporal plate not extending forwards more than half the length of the basisphenoid, with which it is so completely fused in the adult as to be traceable only as a thin line running across the basisphenoid.

The first of these is the most primitive, and agrees precisely with

what is found in the Storks and Herons, Procellariæ, &c. The 2nd and 3rd are modifications of the 1st.

The skull of the first type (Pl. VII. fig. 3) may be regarded as typical of the Steganopodes, and is characterized as follows:—

The palate is desmognathous, the palatines are broad, flattened, and meet in the middle line from the posterior narial aperture backwards to the pterygoids; there is no vomer; the maxillo-palatine processes have become metamorphosed into a spongy mass fusing with a much swollen nasal septum—similar to that of *Balæniceps*—and not extending backwards into the lachrymo-nasal cavity as usual, but yet preserving, as in *P. carbo*, a slight free posterior border; the orbital process of the quadrate is small, styliform, placed at a right angle to the long axis, and about halfway down; the anterior narial apertures are obsolete; and the upper jaw is more or less sharply defined from the skull by a fronto-nasal hinge.

*Phalacrocorax* and *Plotus* belong to this first type, and the above description applies to both; the points whereby the two genera may be distinguished will be found in the appended "key." It may be remarked here, however, that in *Plotus* the maxillo-palatine processes project backwards into the lachrymo-nasal cavity as thin vertical laminæ. There are two points, however, wherein this family differs from the others. Such are the presence of a supraoccipital style and of a "suprajugular." The first is a short, more or less triangular bony rod articulating with a small tubercle on the supraoccipital: the second, as found in *Plotus*, is a more or less elongated, oat-shaped lamina of bone, lying in the lachrymo-nasal fossa, on the jugular process of the maxilla. It was first described, many years ago, by Brandt (3), and appears to have escaped the notice of nearly every writer on the Osteology of this group since. Mr. Beddard refers to it in his recent paper in the P. Z. S. 1888 (1); Fürbringer also refers to it (6). Dr. Gadow writes me that he thinks it is probably "nothing more than an additional splint-bone." I have been wondering whether it is a remnant of a "maxillo-nasal" such as is described and figured in the magnificent monograph on the Dinornithidæ by the late lamented Prof. T. J. Parker. In *Phalacrocorax* it is represented only by a long needle-like splint.

Our second type is found in the skulls of *Phaëthon* and *Pelecanus*, but, beyond this, the two skulls appear to have little else in common.

The skull of *Phaëthon* (Pl. VII. fig. 2) appears to be the least specialized of the whole group, and presents characters which are not only found in all, or nearly all the other Steganopodes, but which also occur in forms outside this suborder. The most important of these is the presence of a large tubular recess lying immediately in front of the quadrate articular surface, and running upwards between the squamosal and prootic bones. In it is lodged the accessory bundle of the temporalis muscle.

This recess is found in *Sula* and *Fregata*, where it is of con-

siderable size; and in *Phalacrocoraæ*, *Plotus*, and *Pelecanus*. Amongst these it is of moderate size only in *Phalacrocorax carbo*; in the other forms it varies, occurring in almost every gradation down to a minute aperture. In *Plotus anhinga* it appears to be wanting altogether. Outside the group it occurs in the *Ciconiæ*, *Procellariæ*, and *Sphenisci*, &c.

The maxillo-palatine processes differ—in the adult at least—from the other Steganopodes, and resemble rather those of the Ibises and Herons, in that they only extend horizontally, and only slightly vertically. They are completely fused throughout the greater part of their extent, but send backwards, into the lachrymo-nasal fossa, two free spongy masses. The nearest approach, as previously hinted, to this arrangement is found in the Ibises and Herons.

Whilst in all the other Steganopodes the palatines are more or less completely fused posteriorly, in *Phaëthon* they are quite free, and in *Fregata* nearly so.

A vomer occurs only in *Phaëthon* and *Fregata*. In the former it is cleft posteriorly; in both, in the adult, it is completely fused posteriorly with the palatines. In *Phaëthon* it is somewhat "knife-blade-shaped," and received between the ends of the maxillo-palatine processes. The dorsal edges of the cleft posterior ends are closely applied to the basisphenoidal rostrum. A bicarinate vomer is found also in the Herons. The vomer is fused with the palatines posteriorly, outside the Steganopodes, in all the other Ciconiiformes, the Anseriformes, Procellariiformes, and Spheniscifformes.

The anterior nares are large, and pervious, in which respect they resemble also those of the Pelicans.

The skull of a nestling *Phaëthon*, prepared under my direction, revealed some very instructive facts, which will be best understood by a reference to the figures (Pl. VIII. fig. 1*a*). That of the ventral view of the skull shows that at this stage the palate is *schizognathous*. The maxillo-palatine processes are small, triradiate, perfectly separate in the middle line, and do not give the slightest promise of the "spongy" nature which they afterwards acquire, when they have fused one with another, to form the desmognathous palate. The aperture of the anterior nares, again, is much larger, and extends farther backwards than in the adult, so much so indeed as nearly to convert the holorhinal into schizorhinal nares. The nasal hinge, so strongly marked a feature in the adult skull, is here conspicuous by its absence. A second skull, somewhat older than this, shows stages intermediate between this and that of the adult.

The skulls of the adult *Pelecanus* and *Phaëthon* do not appear to possess much in common, except the form of the basitemporal plate; but this point is, I think, a rather important one.

The maxillo-palatine processes in *Pelecanus* very closely resemble those of the *Ciconiæ*. They consist of delicately cancellated tissue of considerable vertical extent, extending the whole

height of the upper jaw in fact, and backwards into the lachrymo-nasal fossa, and are of course fused in the middle line ventrally. Seen from behind (Pl. VIII. fig. 6), they are quite distinct one from another. In some specimens, what I take to be traces of an osseous septum nasi are found. As in the Storks, the maxilla and maxillo-palatine processes make up the greater part of the upper jaw. The nasal hinge is generally well marked.

The palatines are completely fused from the posterior narial aperture backwards, and, further, are provided with an enormous dorsal and ventral median keel. A trace of this, as we shall see, is found in *Sula*.

The skull of *Sula*, in the obliteration of the anterior narial apertures, the form of the maxillo-palatine processes and of the palatines, closely resembles that of *Phalacrocorax*. These are some of the latest acquirements of the group, and tend, amongst other things, to single out the two families which they represent as conspicuously "Steganopodous." They may perhaps be regarded as the most intensely modified members of the suborder.

The maxillo-palatine processes of *Sula* differ from those of *Phalacrocorax* in that their coalescence is more complete. Seen from behind, they present an obliquely truncated surface of cancellated or lattice-like tissue, which ventrally does not even extend as far backwards as the posterior end of the maxilla itself. Moreover, a closer examination shows that the bony tissue of the interior of these processes has been more or less completely absorbed, so that the truncated posterior end just described is practically a mere shell or screen concealing the hollow space within. There is no trace of an osseous septum nasi. The palatines are completely fused in the middle line from the posterior narial aperture backwards, and there is a slight median dorsal and ventral keel, just as in *Pelecanus*, but less developed. In *Phalacrocorax* this region of the palatines is rarely, if ever, fused throughout its whole length. An open suture is generally visible. In *Plotus* it appears to be constantly fused. The fronto-nasal hinge is strongly marked.

The basitemporal plate and basisphenoid appear to be an extremely modified form of that obtaining in *Fregata*. The former was very small, not more than half covering the latter, with which it had so completely fused that what should be its free edge is only traceable as a thin faint line. The apertures of the Eustachian tubes appear to have become completely obliterated, leaving only a faint scar on the basisphenoidal rostrum.

*Sula* and *Phalacrocorax* are the only Steganopodes in which the postorbital process is emarginate. This is a common feature amongst the Ciconiæ and Ardeæ, e. g. *Pseudotantalus*, *Nycticorax*, *Cancroma*.

In the skull of a very young nestling *Sula* I found the palate to be *schizognathous*, as in *Phaëthon*, which it closely resembled in the triradiate form of its maxillo-palatine processes. Another point of very considerable significance was the fact that the

anterior narial apertures extended almost the whole length of the upper jaw, while, as has already been remarked, in the adult they are quite obliterated (Pl. VIII. fig. 2).

In the skull of *Fregata* (Pl. VII. fig. 1) the free posterior extremities of the maxillo-palatine processes closely resemble those of *Phaëthon*. They differ, however, markedly in the fact that they extend vertically as well also as horizontally, reaching upwards to the roof of the upper jaw. They are divided by a distinct and osseous septum nasi, swollen dorsally. Vestiges of a precisely similar septum are found in *Phalacrocorax* and *Pelecanus*. There is a long, slender, curved vomer, anteriorly resting upon the posterior ends of the fused maxillo-palatines and posteriorly fused with the palatines. The pterygoid ends of these last, again, are perfectly ankylosed, just as they are in many *Ciconiæ*.

The basitemporal plate in *Fregata*, like that of *Sula*, does not cover the whole basisphenoidal surface. Unlike that of *Sula*, however, it still preserves a free edge, though this is very slight. A short distance in front of the anterior border of this plate, in a slit-like depression of the basisphenoidal rostrum, lie the Eustachian apertures, though so small that only a very slender bristle can be passed through them. If this skull be compared with that of *Sula*, faint traces of the Eustachian tubes in this latter genus will be found, as well as a faint ridge, representing the once free edge of the basitemporal plate.

The nature of the mandibular articular surfaces of the quadrate deserves some notice, since, if this had been adopted instead of the form of the basitemporal plate, and basisphenoid, for the purposes of systematic arrangement, the results would have been almost identical. These surfaces are two in number, the quadrato-jugal and the pterygoid.

In *Phaëthon* and *Pelecanus* the quadrato-jugal surface is directed obliquely outwards and forwards; that of *Pelecanus* being much broader in proportion to its length than that of *Phaëthon*. The pterygoid surface is placed almost at right angles to the long axis of the skull. The two surfaces are divided by a groove, which is most marked in *Pelecanus*. The general impression of the articular end of this bone as a whole is that of a narrow bar continued backward from the pterygoid to the quadrato-jugal bar, which it joins almost at right angles.

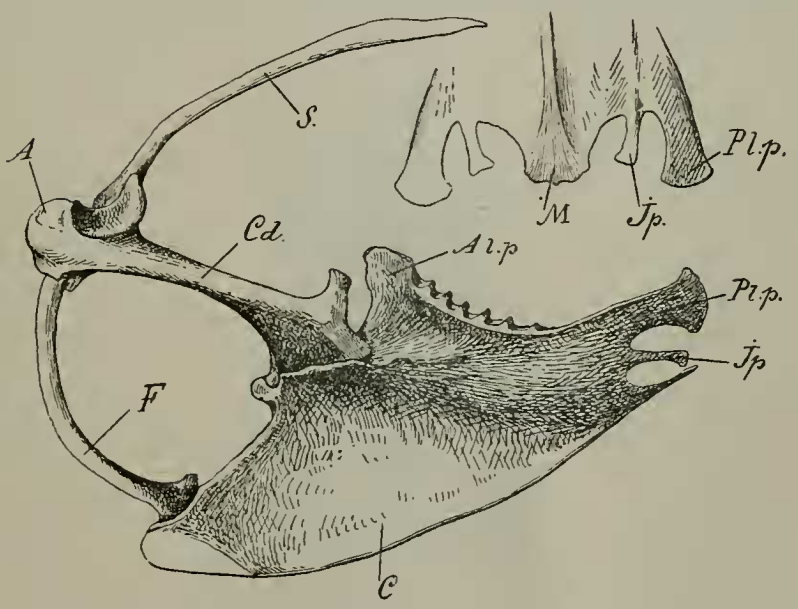
In *Fregata*, *Sula*, and *Phalacrocorax* the surfaces have a V-shaped arrangement. In *Phalacrocorax* the V has almost become U-shaped. The pterygoid surface is subcircular, the quadrato-jugal hour-glass-shaped.

Though the articular surfaces of the quadrate in *Sula* and *Fregata* closely resemble one another, that of *Fregata* can at once be distinguished by the form of the orbital process, which is very large, with a broadly expanded free end resembling that of the Heron. In *Sula*, as in *Phalacrocorax* and *Plotus*, the orbital process is reduced to a small spur standing out at right angles to the long axis of the bone and about halfway down.

The atlas vertebra of the Steganopodes has the odontoid ligament ossified; the neural arch is very broad and flattened, and devoid of a crest. The axis has a fossa immediately underlying the odontoid process, into which pneumatic foramina frequently open. The remaining vertebræ in the different genera and species vary greatly *inter se*, and do not seem to afford any characters which can be regarded as peculiar to the group (see table, p. 99).

In the sternum of the Steganopodes the carina is produced far forwards beyond the *corpus sterni*; it decreases in depth rapidly from before backwards, terminating not far behind the middle of the corpus sterni—save in *Phaëthon* and *Fregata*. The acrocoracoid bears a large facet for articulation with a corresponding facet on the outer side of the dorsal extremity of the furculum. The furculum articulates or is even ankylosed with the carina in *Pelecanus* and *Fregata*.

Fig. 1.

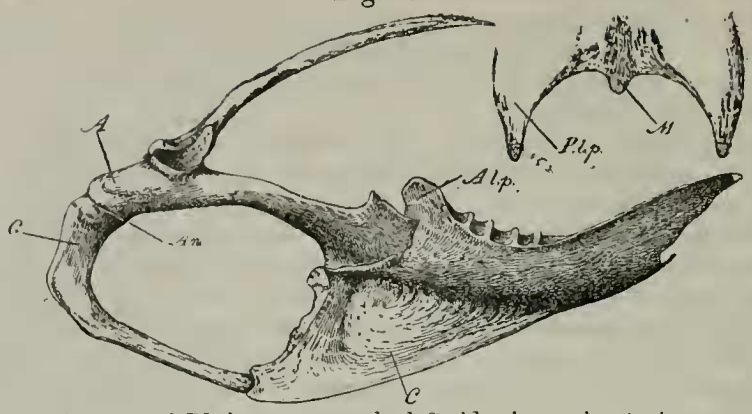



Sternum of *Phaëthon flavirostris*, left side view (nat. size). The small outline immediately to the right represents the form of the posterior border of the sternum, ventral view.

*A.*, Acrocoracoid; *C.*, Carina; *A.l.p.*, Anterior lateral process; *P.l.p.*, Posterior lateral process; *I.p.*, Intermediate process; *F.*, Furculum; *S.*, Scapular; *M.*, Metasternum.

In *Phaëthon* the carina is of the same form, but continued backwards farther than in any other Steganopod save *Fregata*; dorsally the furculum does not articulate with the acrocoracoid by means of apposed flattened facets; ventrally it articulates with the anterior border of the sternum, and not with the extreme antero-ventral angle as in the other forms. The anterior end of

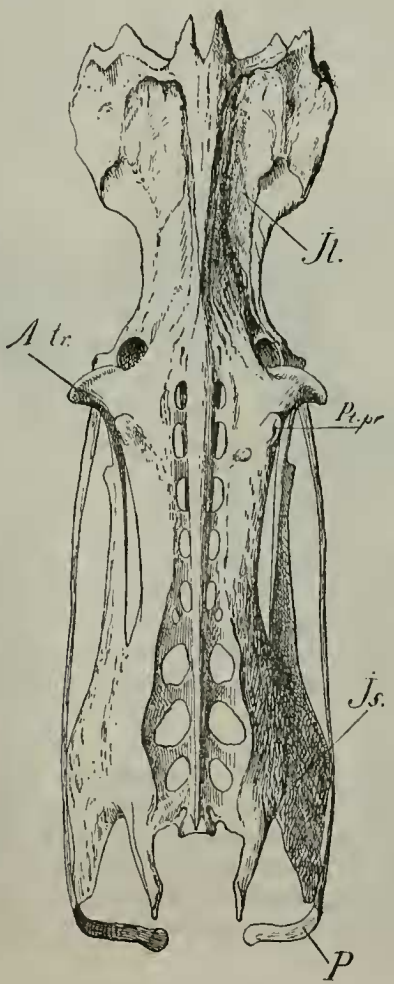
Fig. 2.




Sternum of *Phalacrocorax carbo*, left side view. ½ nat. size.

*C.* Clavicle; *A.n.*, Coraco-clavicular articulation: other letters as in Fig. 1. The small outline immediately to the right represents the form of the posterior border of the sternum, ventral view.

Fig. 3.




Dorsal aspect of the pelvis of *Phalacrocorax carbo*. ⅔ nat. size.

*Atr.*, Antitrochanter; *Il.*, Ilium; *P.*, Pubis; *Is.*, Ischium; *Pt.pr.*, Post-trochanteric process.

the free ventral border of the carina of the sternum is peculiar in that its edge becomes suddenly transformed from a broad to a sharp one, as though it had been shaved off on either side by a knife (see figs. 1, p. 87, & 2, p. 88). The posterior end of the corpus sterni is doubly notched.

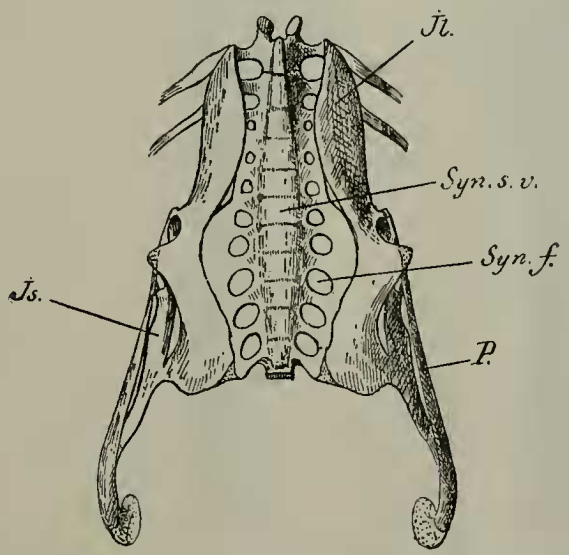
The sternum of *Fregata* is unique in that the furcula is ankylosed dorsally with the acrocoracoid, and ventrally with the carina sterni.

As will be seen by the "key," there are three types of pelvis—that of *Phaëthon* and *Fregata* constituting one, that of *Pelecanus* a second, and those of *Phalacrocorax* and *Sula* a third. This last must be regarded as the typical Steganopodous pelvis (fig. 3, p. 88).

The pelvis of *Pelecanus*, resembles somewhat closely that of *Sula*, and after this, that of the *Anseres*; but differs in the greater width of the preilium, and in that the postilium is not laterally expanded and truncated posteriorly as in the latter group.

The pelvis of *Phaëthon* (fig. 4, p. 89) and of *Fregata* closely resemble one another, and both differ much from that of any other Steganopod. That of *Phaëthon* most nearly resembles that of *Mo-*

Fig. 4.




Dorsal aspect of the pelvis of *Phaëthon flavirostris* (nestling). $\frac{4}{5}$ nat. size.

*Il.*, Ilium; *Syn.s.v.*, Synsacral vertebræ; *Syn.f.*, Synsacral foramen; *P.*, Pubis; *Is.*, Ischium.

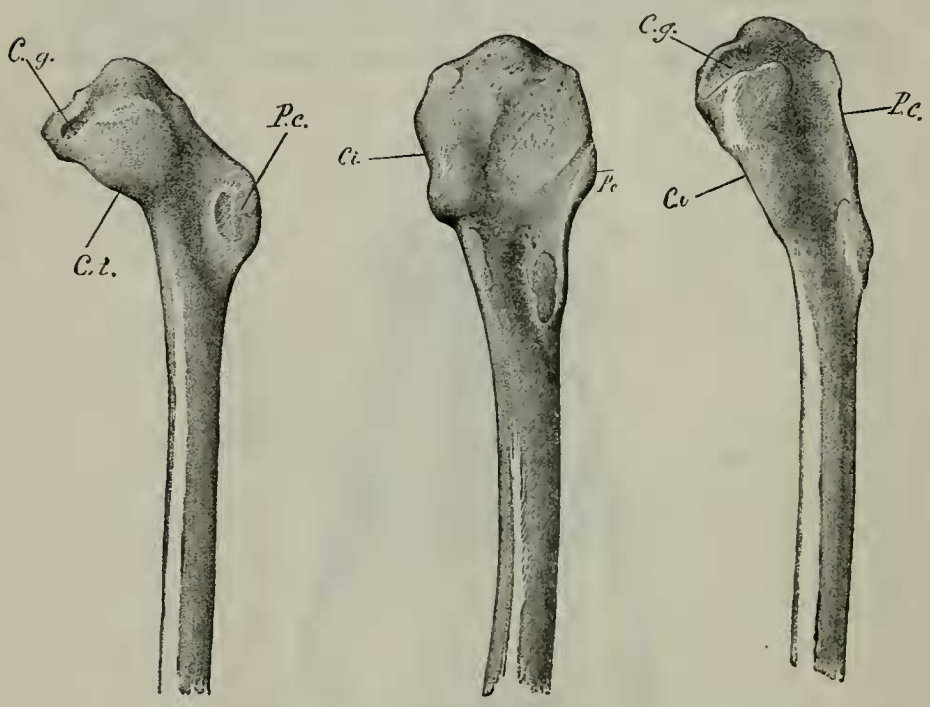
*motus*, but differs therefrom in that the postacetabular ilium is much flattened and bent downwards and outwards, in that the ischium is much longer than broad, instead of being nearly as broad as long, and in the greater length of the pubis. This resemblance can scarcely be regarded as other than an accidental one. What is

more to the purpose is the fact that there are many points of resemblance between the pelvis of *Fregata* and that of certain *Procellariæ*, e. g. *Bulweria*. That this indicates a relationship, though remote, is not improbable. This being so, *Fregata* may be regarded as a link connecting *Phaëthon*, which is undoubtedly one of the least specialized and most primitive of the *Steganopodes*, with the *Procellariiformes*.

The humerus assumes two forms :—

(1) The pectoral crest is triangular in form, and the crista inferior more or less inflated—*Fregata*, *Phaëthon* (fig. 5), *Pelecanus* (fig. 6); and (2) with the pectoral crest represented by a slight ridge but little raised above the level of the shaft, and the crista inferior hardly or not at all inflated—*Sula*, *Phalacrocorax*, *Plotus* (fig. 7).

Fig. 5. Fig. 6. Fig. 7.




Anterior aspects of the proximal end of the humeri of (5) *Phaëthon flavirostris*, nat. size, (6) *Pelecanus rufescens*, $\frac{1}{3}$ nat. size, and (7) *Phalacrocorax carbo*, $\frac{2}{3}$ nat. size.

*C.i.*, Crista inferior; *P.c.*, Pectoral crest; *C.g.*, Coraco-humeral groove.

The forearm and manus offer no characters sufficiently marked to be diagnostic: that of *Phaëthon*, for instance, is not easily distinguishable from that of many *Limicolæ*, and that of *Pelecanus* from that of many *Ciconiæ*.

The pelvic limb of the Steganopodes is peculiar in having a long hallux directed forwards—which, in the living bird, is embraced with the remaining digits in a common web. The tibio-tarsus is inflected distally as in Anseres, some *Rallidæ*, and *Spheniscidæ*.

The tibio-tarsus of *Phaëthon* may be readily distinguished from that of either of the groups just mentioned by the feeble development of its cnemial crests. In the remainder of the Steganopodes the tibio-tarsus can be readily distinguished from that of either the Anseres or *Rallidæ* by the great length of the fibula. This, however, does not apply to the *Spheniscidæ*, in which the fibula is also very long; from that group the Steganopodes can be at once distinguished from the fact that there is a considerable space always visible between the fibula and the tibio-tarsus, running from the lower end of the fibular ridge to the point where the fibula joins the distal end of the tibio-tarsus.

The tarso-metatarsus of *Fregata* resembles that of the Penguins, the three metatarsals being more or less distinct and separated by grooves one from another. It may, however, be readily distinguished therefrom by the fact that the 2nd trochlea is longer than the 3rd and is directed backwards; and by the presence of a foramen between the 3rd and 4th trochleæ.

The tarso-metatarsus in all save *Fregata* is marked by a fossa at the proximal articular end of the anterior surface into which open foramina, pneumatic or otherwise. The hypotarsus is complex in all. Save in *Phaëthon* and *Fregata*, it is characterized by the considerable development of the gastrocnemial ridge.

The object of this paper was to show that the Steganopodes must be regarded as a natural group. Taking *Phalacrocorax* as its type, a fixed point will be gained by which to measure, roughly, the amount of specialization which the various members have undergone. *Plotus* may perhaps be regarded as having passed beyond the mean, it is a highly specialized Cormorant; *Sula* has about reached the level of *Phalacrocorax*: *Pelecanus*, though possessing the peculiar palate of *Phalacrocorax* and *Sula*, is in most other respects less modified; *Fregata* and *Phaëthon* are the lowest members of the group, they represent two divergent branches of a common stem. *Sula*, on account of the form of its basitemporal plate, seems to have affinities with *Fregata* (Pl. VII. fig. 1); *Pelecanus*, for similar reasons, with *Phaëthon* (Pl. VII. fig. 2). All, save *Phaëthon* and *Fregata*, have lost the vomer. Fürbringer and Gadow both agree in regarding *Phaëthon* as the most aberrant of the suborder, and Mr. Beddard goes perhaps further: he writes (1):—"So different are the skull characters of *Phaëthon* from those of the typical Steganopodes that, were it not for *Fregata*, the bird would have to be ignominiously expelled from the order. This catastrophe is averted by *Fregata*, the skull of which, as will have been gathered from the foregoing remarks, serves to link *Phaëthon* with the Cormorants, Gannets, and Pelicans." I cannot but feel, however, that, taking all the skeletal characters into consideration, this family is much more closely allied to the Steganopodes than to that of any other Order. With this the

first part of my paper closes. Whether I have succeeded in the task that I set before me at the beginning of this paper remains for my readers to decide. The accompanying diagram (fig. 8) is an attempt to show the possible lines of divergence within the Suborder, and the probable relationships of the different Families.

Fig. 8.

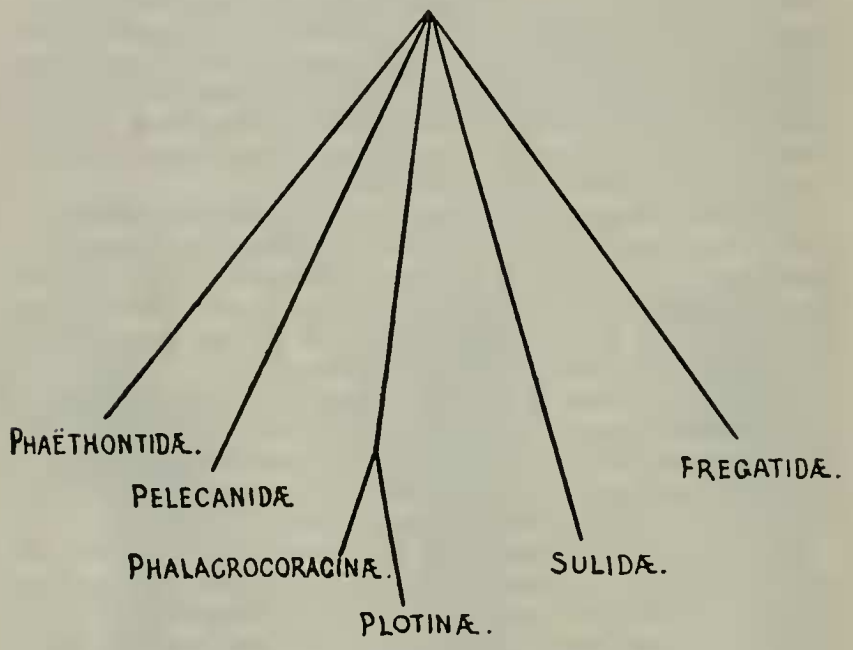



Diagram showing the probable relationships between the various Families of the Suborder Steganopodes.

We must now turn to a question recently raised by Mr. Beddard (1). Are the Steganopodes desmognathous birds? The answer to this, he tells us, depends upon the definition of the term "desmognathous." According to Huxley (10), in the desmognathous skull "the vomer[1] is often abortive, or so small that it disappears from the skeleton. When it exists, it is always slender and tapers to a point anteriorly. The maxillo-palatines are united across the middle line, either directly or by the intermediation of ossifications in the nasal septum."

Those who will turn to Huxley's original paper will find that he considered that the desmognathous skull was to be found "under its simplest form in *Palamedea* and the Lamellirostres. In these birds each maxillo-palatine is a broad, flat, and thin bony

[1] As a matter of fact, the vomer need not be taken into consideration at all.

plate which unites with its fellow in the middle line of the palate." In other words, the maxillo-palatine process represents the internal palatine border of the maxilla. In some Ducks, and in Geese, these processes are prolonged backwards beyond the fused posterior border so as to embrace the vomer between them. Such backwardly directed processes may be further studied in *Ardea*, *Ciconia*, *Accipitres*, *Phaëthon*, and *Fregata* (Pl. VIII. figs. 1 & 4).

It is on account of these backwardly directed processes that Mr. Beddard has been led to ask, "But can *Phaëthon* be accurately termed a desmognathous bird?" Later on he answers it, "*Phaëthon* is really no more desmognathous than is *Æchmophorus* (a schizognathous bird), if we apply the term as Huxley applied it; for the maxillo-palatines in both are widely apart, the vomer lying between them." He continues, "In front of the maxillo-palatines, however, in *Phaëthon* the bony palate forms a continuous platform."

Mr. Beddard's error is, I think, obvious: he has, for the moment, allowed himself to regard the backwardly directed prolongations as if they represented the entire maxillo-palatine process (Pl. VIII. fig. 5). The bony palate which "forms a continuous platform" is really formed by the processes in question, whilst the bones so-called in his paper are but parts of the same.

When discussing the nature of the palate in *Sula* and *Phalacrocorax*, he writes:—"If we are to apply the term desmognathous to these birds, it must be on the understanding that it is a different kind of thing from the desmognathism of—say—the Anseres." His reasons are the following:—the maxillo-palatines in *Phalacrocorax*, *Plotus*, and *Sula* consist of a "thick mass of bone running upwards towards the roof of the skull. Their direction is quite different from the horizontally disposed maxillo-palatine of *Phaëthon*. The conditions observable in the base of the skull of *Fregata* appear to me to clear up this somewhat puzzling discrepancy. In *Fregata*, we have *both the horizontal maxillo-palatines* of *Phaëthon*, separated from each other in the middle line as in that genus, *and the obliquely running 'maxillo-palatines'* of *Phalacrocorax*. As co-existence undoubtedly disproves homology, it seems to me to follow that true maxillo-palatines, comparable to those of other birds, are wanting in *Sula* and *Phalacrocorax*."

I feel perfectly certain that if Mr. Beddard had carefully examined the skull of *Fregata* (Pl. VIII. fig. 4) he would have seen that the horizontal maxillo-palatines and the "obliquely running maxillo-palatines" were both parts of one and the same bone; that the "horizontal maxillo-palatines" were nothing more than backward continuations of the main body of this bone as seen in *Ardea*, &c. This being so, then the maxillo-palatines of *Sula* and *Phalacrocorax* (Pl. VIII. fig. 3) differ only in that they are sharply truncated posteriorly—have no "horizontal" processes. In *Plotus* vestiges of these last yet remain.

*Key to the Osteology of the Steganopodes.*[1]

## A. Skull (Plates VII. & VIII.).

A. Basitemporal plate triangular, its lateral borders fused with the basisphenoid, free anteriorly and contributing to form the mouth of the Eustachian apertures.

*a*. Upper jaw pointed and with a deep nasal hinge; nostrils pervious; palatines separate, embracing a large vomer; lachrymal free; a minute unciform (Beddard) ..... *Phaëthon.*

*b*. Upper jaw very long, depressed, hooked at the tip; nasal hinge imperfect; nostrils impervious; palatines fused in the middle line, with a strong median keel; vomer absent; lachrymal fused ..... *Pelecanus.*

B. Basitemporal plate shield-shaped, with a free edge anteriorly, forming a floor to the Eustachian tubes or grooves; no interorbital septum.

*a*. Aperture of the external nares minute, impervious; palatines meeting in the middle line from the level of the lachrymal backwards, with an ossified supraoccipital style; lachrymal fused with frontal.

*a'*. Upper jaw hooked at the tip; a nasal hinge; lachrymo-nasal fossa large; temporal fossa narrow and deep; suprajugular in the form of a splint-like style; otic process of quadrate lying to the inner side of the squamosal head; orbito-sphenoid incomplete ..... *Phalacrocorax.*

*b'*. Upper jaw pointed; no nasal hinge; lachrymo-nasal fossa partly enclosed by a large suprajugular; temporal fossa very shallow, lateral walls of optic foramen produced forwards to form a tube; otic process of quadrate lying behind squamosal head; orbito-sphenoid complete ..... *Plotus.*

C. Basitemporal plate not extending forwards more than half the length of the basisphenoid, with which it is so completely fused in the adult as to be traceable only as a thin line or ridge running across the basisphenoid.

*a*. Aperture of the external nares almost or quite obliterated; palatines fused in the middle line from the level of the lachrymal backward, with a strong mesial keel; vomer absent; lachrymal fused; postorbital process emarginate, projecting far outwards beyond the cranium; orbito-sphenoid complete, with a nasal hinge; with an interorbital septum. ..... *Sula.*

*b*. Upper jaw strongly hooked at the tip, and concave dorsally; nasal hinge absent; orbital process of quadrate large, expanded at its free end. Aperture of external nares small, impervious; palatines not flattened, fused posteriorly, embracing a long, slender vomer; lachrymal free; with an imperforate interorbital septum. ..... ..... *Fregata.*

## B. Vertebræ.

A. Heterocœlous dorsals.

*a*. First dorsal free, remainder fused one with another, and with the synsacrum, but retaining distinct neural spines and transverse processes; styloid processes of the cervical vertebræ never styliform but fused more or less completely throughout their length either with the pleurapophyseal lamella, or with a lateral ventral lamella from the centrum. Hypapophyses never more than blunt processes, and occur only on the 2nd and 15–18. All the vertebræ are highly pneumatic and pierced by large pneumatic foramina ..... *Pelecanus.*

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[1] The "keys" appended are designed for the use of those desirous of determining—at least generically—parts of skeletons which may be either undetermined or doubtfully named; they are not meant to express the systematic relations of the various genera—save that of the skull. "Keys" to the genera can easily be compiled from these.

*b.* All the dorsals free; styloid processes short and blunt on all the cervical vertebræ from the fifth backwards; 5th to 7th vertebræ with a slender bony bar from the metapophysis backwards to the hyperapophysis, neural crests present only on the second, third, and fourth. Hypapophyses on the second and third cervicals, and from ninth cervical backwards to the synsacral vertebræ, longest on the dorsals ... *Phaëthon.*

B. Opisthocœlous dorsals, all of which are free.

*a.* Hypapophyses present only on cervicals 1–3. All cervicals, save atlas and axis, bear styloid processes; meta- and hyperapophyses feebly developed; hæmal arches absent ..... *Fregata.*

*b.* Hypapophyses present, on cervicals 1–4 very large, on 17–18 very feeble. Styloid processes from vertebræ 1–12; those of 8–10 long and slender. Hæmal arches to vertebræ 8–12; distinct metapophyses from 4–13, from 7–11 large; no synsacral or dorsal hypapophyses ..... *Sula.*

*c.* Hypapophyses 1–3 and 13–23 very large, compressed. Synsacral hypapophyses 4, decreasing in size backwards; hypapophyses 3–6 in the form of a median ridge; distinct styloid processes on all the vertebræ from 3–12, from 8–10 long, slender, those of the 9th extending as far back as the posterior articular surface of the centrum; no complete hæmal arches; neural crests from 2–7 distinct, in form of sharp ridges; hyperapophyses 3–10 very distinct: centrum elongated and compressed; 16–18 cervicals much flattened ventrally ..... *Phalacrocorax.*

*d.* Hypapophyses of atlas and 15–16 large, those of the two latter much compressed; those of the 2nd and 19–21 and 23rd in form of a low median ridge, that of the 22nd with lateral expansions ventrad. Synsacral hypapophyses 3, the 3rd vestigial. Anapophyses of 9–14 forming closed canals. Centra 3–13 *grooved ventrally.* Styloid processes 2–10 and 13–15 distinct, those of 8, 9, 10 long and slender, 8th extending as far back as the level of the posterior articular surface of the centrum; neural crests slightly developed; *anterior vertebræ with much elongated cylindrical centra* ..... *Plotus.*

## C. Sternum and Pectoral Girdle (figs. 1 & 2, pp. 87 & 88).

A. The free end of the clavicle not provided with a facet for articulation with the acrocoracoid; the furcular apophysis of the clavicle articulating with the anterior border of the carina sterni, and not with its antero-ventral angle. Carina sterni and region of corpus sterni bearing coracoid grooves not produced far beyond the level of the costal process of the sternum. Carina extending nearly the whole length of the corpus sterni, the posterior border of which is doubly notched (=posterior lateral and intermediate processes). Coracoids touching, with a supracoracoid foramen and large precoracoid process ..... *Phaëthon.*

B. The free end of the clavicle with a facet for articulation with the acrocoracoid; and the furcular apophysis of the clavicle articulating with the antero-ventral angle of the carina sterni. Coracoids widely separate; no intermediate process to posterior border of the sternum.

*a.* Greater part of carina sterni and region of sternum bearing the coracoid grooves produced far forward beyond the anterior lateral processes of the sternum. Precoracoid well developed; no supracoracoid foramen ..... *Sula.*

*b.* Less than half the carina lying beyond the level of the anterior lateral process of the sternum, the inner angle of the outer border of which is continuous with the outer angle of the coracoid groove.

*a'.* Furculum fused with carina sterni; carina about three-fourths the length of the corpus sterni; precoracoid well developed; a supracoracoid foramen ..... *Pelecanus.*

*b'*. Furculum not fused with carina sterni; precoracoid feebly developed.

*a*$^2$. Carina scarcely extending beyond the middle of the corpus sterni. *Phalacrocorax.*

*b*$^2$. Carina three-fourths as long as corpus sterni ..... *Plotus.*

O. Sternum broader than long, carina extending the whole length of corpus sterni. Furculum fused dorsally with the head of the coracoid and ventrally with the carina sterni ..... *Fregata.*

## D. Pelvic Girdle (figs. 3 & 4, pp. 88 & 89).

A. Pelvis nearly as broad as long. Ilia widely separated one from another by the transverse processes of the synsacrum. Preilium narrow, postilium presenting a broad surface dorsally; about half of the total length of the pubis free, projecting beyond the postero-inferior angle of the ischium. Obturator foramen about twice the diameter of acetabulum.

*a*. Anterior and posterior renal fossæ separated one from another by a low ridge, and not divided up into compartments by ventral transverse processes of the synsacrum ..... *Phaëthon.*

*b*. Posterior renal fossa separated into a number of narrow compartments by the ventral transverse processes of the synsacrum ..... *Fregata.*

B. Pelvis much longer than broad. Preilia meeting in the mid-dorsal line, postilia not widely separated and presenting a broad dorsal surface.

*c*. Pelvis more than twice as long as broad; dorsal surface of postilium very broad. Ischiadic foramen about three times as long as the diameter of the acetabulum. Preilium of about equal width throughout, postilium presenting a broad dorsal surface; rather less than a fourth of the total length of the pubis free and projecting beyond the postero-inferior angle of the ischium, almost directly backwards. Anterior renal fossa deep, its length equal to the depth of the ischiadic foramen. Obturator foramen nearly closed by bone ..... ..... *Pelecanus.*

*d*. Pelvis about three times as long as broad; dorsal surface of postilium moderately broad.

*a'*. Ischiadic foramen nearly or quite five times the diameter of the acetabulum.

*a*$^2$. Preilium of about equal width throughout or with a very slight expansion cephalad; postilium presenting a moderately broad dorsal surface; about one-third of the total length of the pubis projecting beyond the postero-inferior angle of the ischium. Anterior renal fossa deep, moderately wide, length nearly or quite equal to the depth of the ischiadic foramen. Obturator foramen nearly or quite surrounded by bone..... *Sula.*

*b*$^2$. Preilium much expanded cephalad; about one-fourth total length of the pubis free, and turning downwards and inwards almost at a right angle at the postero-inferior angle of the ischium. Anterior renal fossa extremely narrow, length about equal to the depth of the ischiadic foramen. Obturator foramen not shut off from obturator fissure by bone ..... *Phalacrocorax.*

*b'*. Ischiadic foramen about twice as long as acetabulum. Preilium much expanded cephalad; inferior border notched; dorsal surface of postilium with its outer border forming a thin raised edge to the dorsum of the pelvis; with a strong ridge from the post-trochanteric process forwards to meet its fellow in the middle line; about one-fourth of the total length of the pubis projecting beyond the postero-inferior angle of the ischium; anterior renal fossa small, pyriform. Obturator foramen nearly or quite shut off from the obturator fissure. *Plotus.*

## E. Pectoral Limb (figs. 5–7, p. 90).

A. All the bones of the wings pneumatic.

*a*. Ulna with a large pneumatic foramen lying on the palmar surface distad of the glenoid cavity.

*a'*. Humerus nearly as long as the ulna (in the articulated wing the arm is nearly as long as the forearm). Sub-trochanteric fossa large, continued cephalad under capitulum of humerus as a large pneumatic foramen, into which open numerous small foramina. Crista inferior (ulnar tuberosity) with anterior surface much inflated, and sharply defined from the shaft, distad, by a groove. Coraco-humeral groove a shallow depression. Pectoral crest (radial tuberosity) triangular, of moderate size. Insertion of brachialis anticus well-defined; with a pneumatic foramen above condylus ulnaris. Radius with a faint depression over the dorsal aspect of the expanded distal end. Manus having the carpo-metacarpus three times the length of Ph. 2. D. II. Ph. 1. D. II. with two deep and sharply defined postaxial depressions. Ph. 1. D. III. with a well-marked triangular postaxial border. ..... *Pelecanus.*

*b'*. Humerus about one-fifth less than the ulna (in the articulated wing the arm is less than the forearm). Sub-trochanteric fossa not overhung by tuberculum inferius, otherwise resembling that of *Pelecanus*. Crista inferior inflated, but less sharply defined from the shaft. Coraco-humeral groove deep and narrow; triangular form of the radial tuberosity (pectoral crest) very large. Depression for brachialis anticus with a pneumatic foramen proximad of radial condyle. Radius with a deep depression over the superior border of the distal articular end. Manus having the carpo-metacarpus little more than twice length of Ph. 2. D. II. Postaxial ledge of Ph. 1. D. II. with two shallow depressions. Ph. 1. D. III. with the triangular postaxial border slightly developed ..... *Fregata.*

*b*. Ulna with a very shallow depression in place of a pneumatic foramen. Humerus less than ulna (in the articulated wing the arm nearly equals forearm). Sub-trochanteric fossa overhung by tuberculum inferius, and running up as a pneumatic foramen into the caput humeri. Crista inferior flattened, passing gradually into the shaft. Coraco-humeral groove deep. Pectoral crest triangular, size moderate; depression for brachialis anticus not well-defined, without a pneumatic foramen. Manus having carpo-metacarpus less than twice length of Ph. 2. D. II. *Phaëthon.*

*c*. Ulna with a distinct palmar and interglenoid pneumatic fossa. Humerus longer than ulna (in the articulated wing the arm is one-fifth longer than forearm). Sub-trochanteric fossa overhung by tuberculum inferius and running up as pneumatic foramen into caput humeri. Crista inferior slightly swollen, moderately defined from the shaft. Coraco-humeral groove shallow. Pectoral crest in the form of a long low ridge but little raised above the shaft. Depression for brachialis anticus well-defined and without a pneumatic foramen. Metacarpus nearly or quite as long as Ph. 2. D. II. ..... *Sula.*

B. Wing-bones not pneumatic: pectoral crest a low ridge.

*d*. Crista inferior passing insensibly into shaft. Sub-trochanteric fossa deep, pneumatic foramen absent. Ulna equal or nearly equal in length to the humerus (in the articulated wing the arm shorter than forearm), with the border of the glenoid cavity for the radial condyle of the humerus produced into a hook-like process. Manus much shorter than ulna. Mc. III. very slightly arched; Ph. 1. D. II. with a deep ventral fossa. *Phalacrocorax.*

*e*. Crista inferior with its free border arched, distinct from shaft, with a slight depression in place of the sub-trochanteric fossa. Ulna shorter than humerus (in articulated wing forearm shorter than arm); hook-like process of glenoid cavity of radial condyle of humerus but slightly developed. Manus equal, or nearly equal, to that of ulna. Mc. III. not arched; Ph. 1. D. II. with a shallow ventral depression. ..... *Plotus.*

### F. Pelvic Limb.

A. Fibula never more than three-fourths as long as the tibio-tarsus.

*a*. Femur with a deep popliteal depression: tibio-tarsus with moderately well-developed ento- and ectocnemial crests. Fibular ridge well-marked, extending downwards to within a short distance of the middle of the shaft. Tarso-metatarsus with a large pneumatic foramen on the inner side of its proximal end; hypotarsus with a vertical ridge having a moderate backward extension, the free edge of which is expanded into a flattened surface; on the outer side of the ridge lie two closed canals: with a deep fossa above the insertion of the tibialis anticus leading into two large pneumatic foramina. Middle toe shorter than tarso-metatarsus ..... *Pelecanus.*

*b*. Femur without a popliteal depression: tibio-tarsus with feebly developed ecto- and entocnemial crests. Fibular ridge absent. Tarso-metatarsus deeply grooved anteriorly, the groove leading directly into the foramen between the third and fourth trochleæ; gastrocnemial ridge feebly developed. Middle toe longer than the tarso-metatarsus ... *Phaëthon.*

B. Fibula extending downwards to the level of the external articular condyle of the tibio-tarsus.

*c*. Femur with a fossa at the base of the great trochanter into which numerous pneumatic foramina open: tibio-tarsus with moderately developed ento- and ectocnemial crests. Fibular ridge well-marked. Tarso-metatarsus grooved anteriorly; with numerous pneumatic foramina immediately above the insertion of the tibialis anticus. Gastrocnemial ridge moderately well-developed ..... *Sula.*

*d*. Femur without pneumatic foramina. Tarso-metatarsus slightly grooved anteriorly, with a deep fossa above the insertion of the tibialis anticus, at the bottom of which lie two foramina which pierce the shaft and emerge on either side of the gastrocnemial ridge. Fibular ridge very strong.

*a'*. Tibio-tarsus with strong ecto- and entocnemial crests, the latter reflected outwards. Gastrocnemial ridge very large, its free border expanded into a flattened surface. Tarso-metatarsus comparatively slender, length greater than that of the 2nd toe. Patella large, conical. *Phalacrocorax.*

*b'*. Tibio-tarsus with the free edge of the entocnemial crest looking straight forward, not reflected outwards. Gastrocnemial crest moderately well-developed. Tarso-metatarsus short and broad, length less than that of the 2nd toe. Patella flattened, with a groove running obliquely across the middle for the tendon of the ambiens ... *Plotus.*

C. Fibula fourth-fifths as long as tibio-tarsus. Femur nearly as long as fibula, very thick relatively to the tibio-tarsus, and highly pneumatic; with a popliteal fossa containing a pneumatic foramen. Tibio-tarsus non-pneumatic; cnemial crests feeble; fibular crest feeble. Tarso-metatarsus extremely short, resembling that of the Penguins, the three metatarsals being indicated by grooves; the length of the tarso-metatarsus one-third greater than the width measured across the trochleæ ..... *Fregata.*

*Phalacrocorax* and *Sula* have each a free sternal rib attached to the posterior border of the last thoracic vertebra.

The vertebral column of *Pelecanus* is peculiar in that, of the thoracic vertebræ, only the 1st is free, the remainder being fused one with another and with the synsacrum. The transverse processes of the 2nd, 3rd, and 4th have ankylosed one with another, and the whole is fused with the anterior border of the preilium, so that, at first sight, it would appear as though this extended as

*Tabular arrangement of the Vertebral Column*: after Parker, Phil. Trans. 1891, p. 78 (see above, p. 87).

S. sc.

Cv. 16 : Cv. Th. 2 : Th. $\underbrace{3+2}_{5}$ : Lb. 4 : Lb. Sc. 3 : Sc. 2 : $\underbrace{\text{Cd. } 8+8}_{16} = 48$ ..... *Phalacrocorax.*

S. sc.

Cv. 18 : Cv. Th. 2 : Th. $\underbrace{3+3}_{6}$ : Lb. 4 : Lb. Sc. 2 : Sc. 2 : $\underbrace{\text{Cd. } 5+8}_{13} = 47$ ..... *Plotus.*

S. sc.

Cv. 17 : Cv. Th. 1 : Th. $\underbrace{4+2}_{6}$ : Lb. 4 : Lb. Sc. 2 : Sc. 2 : $\underbrace{\text{Cd. } 4+9}_{13} = 45$ ..... *Sula.*

S. sc.

Cv. 16 : Cv. Th. 1 : Th. $\underbrace{1+3+1}_{4}$ : Lb. 3 : Lb. Sc. 4 : Sc. 2 : $\underbrace{\text{Cd. } 4+7}_{11} = 42$ ..... *Pelecanus.*

S. sc.

Cv. 12 : Cv. Th. 2 : Th. $\underbrace{5+1}_{6}$ : Lb. 3 : Lb. Sc. 2 : Sc. 2 : $\underbrace{\text{Cd. } 5+7}_{12} = 39$ ..... *Fregata.*

S. sc.

Cv. 11 : Cv. Th. 3 : Th. $\underbrace{6+1}_{7}$ : Lb. 2 : Lb. Sc. 2 : Sc. 2 : $\underbrace{\text{Cd. } 3+9}_{12} = 39$ ..... *Phaëthon.*

far forward as the 1st thoracic vertebra. The last sternal rib has a posterior expansion situated immediately behind the articulation with its dorsal element.

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## EXPLANATION OF THE PLATES.

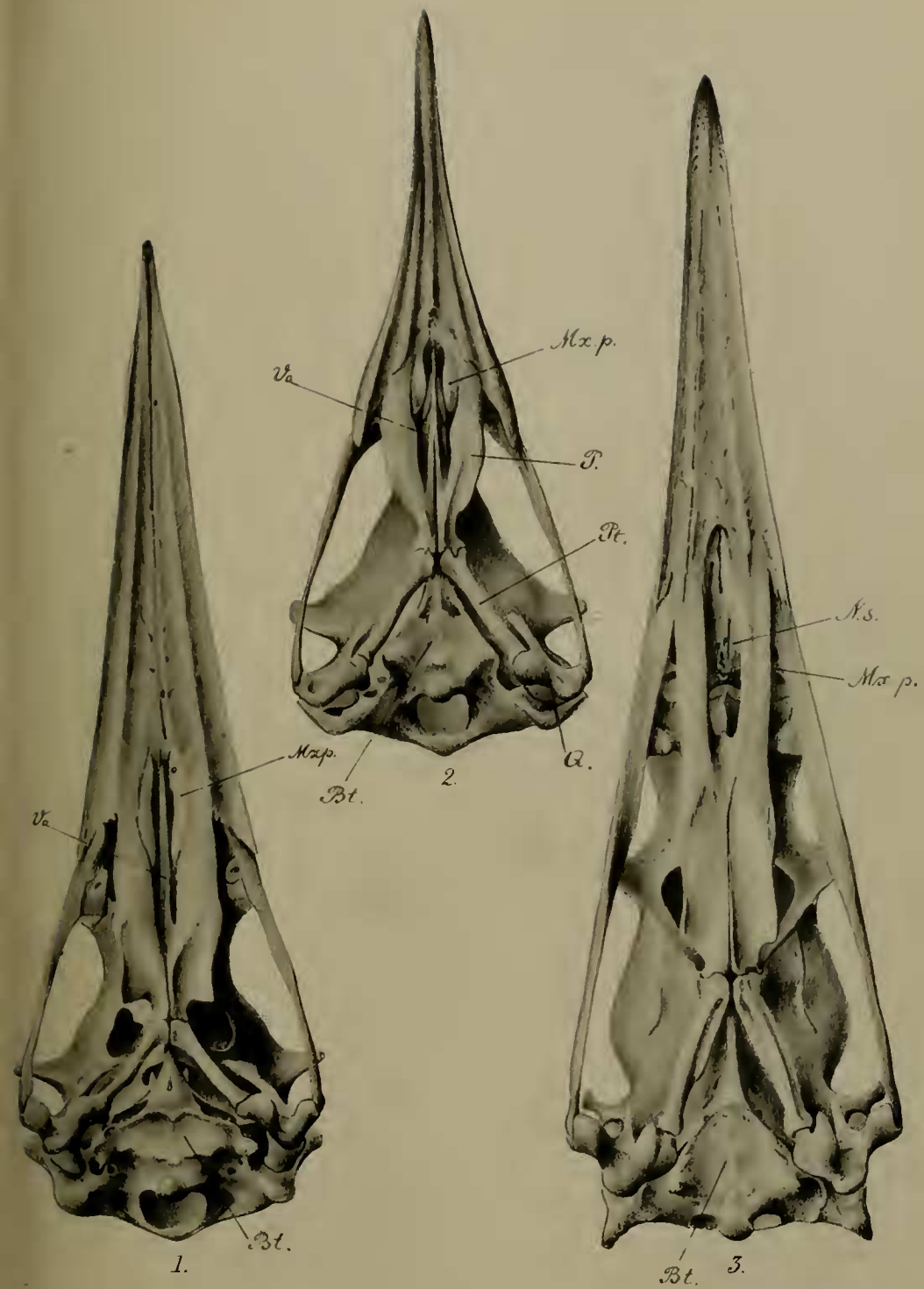
*B. pl.*=Basitemporal plate.
*Mxp.*=Maxillo-palatine process.
*Ns.*=Nasal septum.
*P*=Palatine.
*Pt.*=Pterygoid.
*Q*=Quadrate.
*V*=Vomer.

### Plate VII.

Fig. 1. Ventral view of the skull of *Fregata ariel*, showing the form of the basitemporal plate, the maxillo-palatine processes, and the ankylosis of the posterior ends of the palatines.

Fig. 2. Ventral view of the skull of *Phaëthon flavirostris*, showing the same as fig. 1. The posterior ends of the palatines, though closely approximated, are not fused.

Fig. 3. Ventral view of the skull of *Phalacrocorax carbo* showing the same as the above. The palatines are here more or less fused from the posterior narial aperture backwards to the pterygoids. There is no vomer.




H Grönvold del. Photoprint by Bale. Danielsson Ltd

OSTEOLOGY OF STEGANOPODES.

*1. Fregata ariel. 2. Phaëthon flavirostris.*

*3. Phalacrocorax carbo.*